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LATE DEVONIAN FRESH-WATER FISHES
FROM THE
WESTERN UNITED STATES

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FIELDIANA: GEOLOGY

VOLUME 11, NUMBER 5

Published by

CHICAGO NATURAL HISTORY MUSEUM
DECEMBER 28, 1951

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UNIVERSITY OF ILLINOIS

PRINTED IN THE UNITED STATES OF AMERICA
BY CHICAGO NATURAL HISTORY MUSEUM PRESS

INTRODUCTION

During the geological exploration of the western United States, occasional finds of fossil fishes have been made in Late Devonian rocks. Some of these have received only casual mention in geological reports. Others, though identified by vertebrate paleontologists, have not been adequately studied, probably because the remains are fragmentary and thus in many cases identification even to family is difficult. In the summer of 1949 I visited most of the sites at which Late Devonian fishes have been reported in Arizona, Colorado, Wyoming, and Utah. Although most of the specimens obtained were poorly preserved, a study of the collections revealed the inadequacy of the earlier work. For a clearer picture of the Devonian fishes of this period, and the conditions under which they were preserved, a revision seemed desirable. This has been made as complete as possible, although a few of the early collections have not been seen.

The earliest discovery of Late Devonian fishes in the western United States was made in 1874 in southwestern Colorado by Endlich (1876, p. 212) of the Hayden Survey. Endlich's material and more collected later by Cross in the same rocks, the Elbert formation, were described by Eastman (1904, pp. 253-258), who referred them to *Bothriolepis* and *Holoptychius*. In 1879, Walcott (1880, p. 225) discovered some "placoganoid fishes" in a Devonian sandstone in Kanab Canyon, Arizona. These fragmentary remains from what came to be called the Temple Butte formation, were identified by Gidley (Schuchert, 1918, p. 361) as *Bothriolepis* and *Holoptychius*. Another early discovery was made in 1896 by Tower, who found fish remains in the Late Devonian Parting Quartzite near Aspen, Colorado. The teeth in this collection were referred to crossopterygians by Girty (Spurr, 1898, p. 21), and other fragments were referred doubtfully to lung fishes and arthrodires by Eastman (1904, pp. 258-259). In 1912, Worcester collected some fossils at Fossil Ridge, Gunnison County, Colorado, in strata supposed to be of Ordovician age. The fishes in this collection were briefly noted by Cockerell (1913, pp. 246-247), who was able to identify them as *Coccosteus*, *Rhizodus* and *Diplacanthus*, and still maintain

that they were Ordovician. As will be shown below, Cockerell was mistaken both in his identification of the fossils and in their age.

In more recent years, a number of occurrences of Late Devonian fishes have been reported. Several of them are in the Parting member of the Chaffee formation of central Colorado (Behre and Johnson, 1933; Bryant and Johnson, 1936; Johnson, 1944). Fishes have also been reported from the Darby formation of Wyoming (Branson, 1929; Branson and Mehl, 1930; Baker, 1946). Descriptions of the Darby fishes have never been published, but as will be shown below, they are of Late Devonian fresh-water types. This is also true of the fishes from what was identified as the Leigh member of the Bighorn formation (Foster, 1947). Since the Leigh is Late Ordovician in age, it is clear that part of the Darby formation has been misidentified here.

Typically marine Late Devonian fishes will not be considered in this work. These have been reported in the Sly Gap formation of western New Mexico (Colbert and others, 1950), and in the Ouray, Picacho de Calera, and Martin formations of eastern Arizona and southwestern Colorado (Hay, 1902; Stoyanow, 1936, 1942). The Jerome formation of central Arizona (Hussakof, 1942; Stoyanow, 1926, 1936), which includes a near shore marine facies with a mixed marine and fresh-water fish fauna, will be considered at another time. The Jefferson formation is marine, but the lung fish teeth that have been found in it in Montana and Utah will be discussed because of the possibility that they were of fresh-water origin. The reported occurrence of fish remains in the lower part of the Jefferson formation of south central Idaho (Ross, 1934, 1937) is misleading. The fish are of Early Devonian types, and so the rocks in which they occur must represent a formation distinct from the Jefferson.

This study is based in large part on collections I made in 1949 and 1950 in Colorado, Wyoming, and Utah, for Chicago Natural History Museum. In addition, Dr. David H. Dunkle of the United States National Museum has generously made it possible for me to study many of the early collections of members of the United States Geological Survey. A small collection from the Darby formation of Teton Pass, Wyoming, has been made available by Dr. Claude W. Hibbard of the Museum of Paleontology, University of Michigan. Except as otherwise noted, the specimens described are in the collections of Chicago Natural History Museum. The drawings were made by Mr. John Conrad Hansen, Artist in the Department of Geology, and me, mostly from my original sketches.

ANTIARCHI

The peculiar armored placoderm, *Bothriolepis*, is a characteristic element of Late Devonian fresh-water faunas throughout much of the world. It is common in the western United States, but its remains are usually fragmentary or poorly preserved, so that identification is difficult. Two species are to be distinguished in this area.

Bothriolepis coloradensis Eastman: The original description of this species by Eastman in 1904 was based on material collected by Cross in southwestern Colorado. Stensiö (1931, p. 11; 1948, p. 224) concluded from Eastman's figures with some justification that it did not belong to *Bothriolepis*, but to the Remigolepidae. Eastman's figures, however, are quite inadequate to characterize this form, and a study of the type, as well as new material collected for Chicago Natural History Museum, clearly shows that this is *Bothriolepis* and possibly a valid species.

Stensiö referred this species to the Remigolepidae because Eastman's figures (1904, figs. 1, 4) suggest that the pectoral fin was not divided into two articulated segments. The type (U.S.N.M. no. 16852) is a ventral trunk shield exhibiting the inner surface, with fragments of both pectoral appendages in place. The more complete appendage, that of the left side, does not preserve the articulation, but shows quite convincingly that one was present between proximal and distal segments. The ventral central plate 2 and the lateral marginal plate 2 are recognizable and show the beginnings of the taper towards the articulatory area, exactly as in *Bothriolepis*. A second specimen in the United States National Museum, originally on the same slab of rock as the type, preserves a distal segment of a pectoral fin of the *Bothriolepis* type. Thus it is certain that this form does not belong to a remigolepid, as Stensiö suspected.

Since Cross's collections were made, no additional specimens have been found at the type locality, one mile south of Rockwood, La Plata County, Colorado. The Elbert formation does not outcrop here, and the original finds were made in talus below its presumed occurrence. A number of specimens of *Bothriolepis* have been found both by Cross and by me 11½ miles to the east on Endlich Mesa, where the Elbert formation is well exposed. Eastman identified an incomplete proximal fin segment from this locality as *B. coloradensis* because of its large size. Other fragments he referred to *B. "leidyi"* (= *B. nitida*) largely because of their smaller size and presumed differences in ornamentation. Size, of course, is not a reliable specific character, and, as will be shown below, Eastman

probably misinterpreted the ornamentation of the Rockwood specimens. In 1949, I found fragmentary remains of *B. coloradensis* eight miles north of Rockwood in a limestone in the Elbert formation. This is the locality described by Cross (1904, p. 250) on Little Cascade Creek, about one-half mile south of Columbine Lake. It is probable that all of the *Bothriolepis* remains from this region in southwestern Colorado belong to *B. coloradensis*, and it is possible with the additional material now available to characterize the species somewhat better, though not completely.

Size: Eastman distinguished *B. coloradensis* in part by its large size. It is true that this species does attain a moderately large size for the genus, but measurements of a few individuals have little significance. For example, the antero-median-dorsal plates (AMD) of *B. canadensis* in the Dartmouth College Museum have lengths ranging between 14.3 and 74 mm., depending on the age of the individual. The two antero-median-dorsal plates of *B. coloradensis* in Chicago Natural History Museum are 58 mm. and 62 mm. long, corresponding in size to the large mature *B. canadensis*. The width of the ventral armor of *B. coloradensis*, measured at mid-length, is 85 mm. (Eastman, 1904, p. 256), but this may be exceeded by very large *B. canadensis*. It is clear then that these two species cannot be distinguished by their size.

Ornamentation: Eastman described the superficial ornamentation of the specimens from Rockwood, Colorado, as clearly tuberculate, with the tubercles more or less confluent, but not forming vermiculating ridges. The type, however, shows mainly the inner side of the ventral armor and is entirely inadequate to indicate the character of the ornamentation. This feature is shown much better in material from Endlich Mesa and Little Cascade Creek (fig. 40, D, E). These specimens show that, compared to *B. canadensis* of equal size, the ornamentation is not coarser, as Eastman said, but about the same. It does differ, however, from *B. canadensis*, and resembles *B. cellulosa* in being reticular, with very slight or no tubercular elevations at the anastomoses of ridges. In parts of certain plates, as, for example, on the medial part of the lateral plate (fig. 40, D), the even reticular arrangement gives way to a more ridged type of ornamentation, with the ridges straight or sinuous. Reticular ornament is characteristic of juvenile individuals of most species of *Bothriolepis*, as Stensiö has pointed out (1948, p. 212), but it is clear that in the known specimens of *B. coloradensis* we are dealing with parts of fully adult individuals.

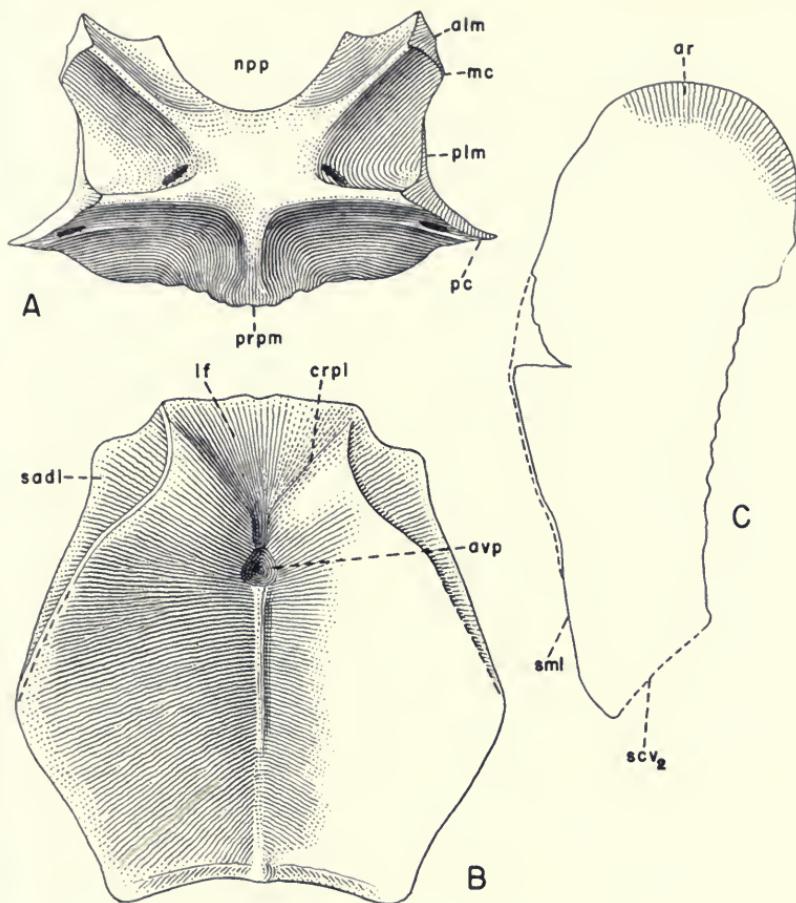


FIG. 38. *Bothriolepis coloradensis* Eastman (natural size). A, Centro-nuchal plate, restored from PF 591, Chaffee formation, Gunnison County, Colorado. B, Antero-median-dorsal plate, restored from PF 360, Elbert formation, La Plata County, Colorado. C, Right ventral central plate, PF 593, Chaffee formation, Gunnison County, Colorado. *alm*, anterior division of lateral margin; *ar*, articular area; *avp*, anterior ventral pit; *crpl*, post-levator crest; *if*, levator fossa; *mc*, lateral corner between anterior and posterior divisions of lateral margin; *npp*, post-pineal notch; *pc*, postero-lateral corner; *plm*, posterior division of lateral margin; *prpm*, postero-median process; *sadl*, area overlapping antero-median-dorsal plate; *scv*₂, suture for second ventral central plate; *sml*, suture for lateral marginal plate.

Plates of the carapace: The only known plate of the head shield is the lateral plate (PF 364, fig. 40, D), which agrees with the same plate of *B. canadensis* and *B. cellulosa*. The antero-median-dorsal plate (AMD; fig. 38, B) resembles in most respects that of *B. canadensis* and *B. cellulosa*. It differs from these species in that the

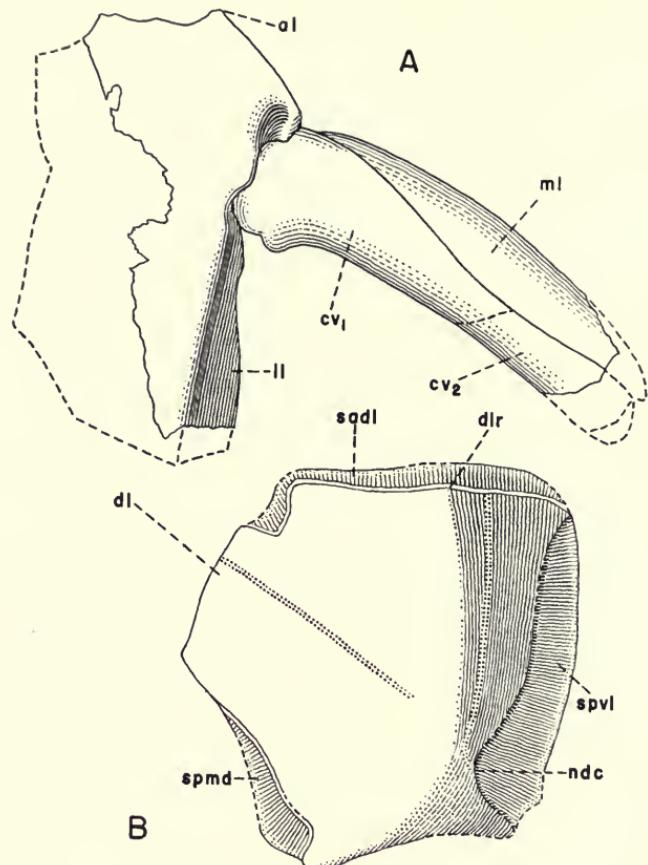


FIG. 39. *Bothriolepis coloradensis* Eastman, Elbert formation, Endlich Mesa, La Plata County, Colorado ($\times \frac{3}{4}$). A, Left antero-ventro-lateral plate and proximal segment of pectoral fin, restored from PF 355. B, Right mixilateral plate, PF 357. *al*, antero-lateral corner; *cv*₁, *cv*₂, first and second ventral central plates; *dl*, dorsal lamina; *dlr*, ridge between dorsal and lateral laminae; *ll*, lateral lamina; *ml*, lateral marginal plate; *ndc*, notch for dorsal corner of postero-ventro-lateral plate; *sadl*, area overlapped by antero-dorso-lateral plate; *spmd*, area overlapped by postero-median-dorsal plate; *spvl*, area overlapped by postero-ventro-lateral plate.

post-levator crests nearly meet in front of the anterior ventral pit, resulting in a shorter and relatively broader levator fossa (fig. 38, B, *lf*). The anterior border of the antero-median-dorsal plate is relatively short, even shorter than the posterior border, which differs from the situation in *B. canadensis* and *B. cellulosa*. The postero-median-dorsal plate agrees well with that of *B. canadensis*. The mixilateral plate (MXL; fig. 39, B) indicates that the lateral walls

of the trunk shield were relatively high. The length/height of its lateral lamina is 2.4, about the same as in *B. canadensis* and *B. cellulosa*.¹

The dorsal lamina is very broad, its length/width ratio being 1.4, compared to a corresponding ratio of 1.5 to 2.0 in *B. canadensis* and *B. cellulosa*. This broad dorsal lamina may signify a slightly broader trunk armor than in the latter species, or a greater angle between the dorsal and lateral walls of the trunk armor; the angle could not be measured because of crushing. The anterior border of the mixilateral plate, that is, the ornamented part that meets but is not overlapped by the antero-dorso-lateral plate (ADL), is nearly straight, not concave as in *B. canadensis* and *B. cellulosa*. The notch in the posterior part of the ventral border (fig. 39, B, *ndc*) that received the dorsal corner of the postero-ventro-lateral plate (PVL) is rounded and agrees closely with that of *B. canadensis*. The antero-ventro-lateral plate (AVL; fig. 39, A) resembles that of *B. canadensis*. Judging from Eastman's description and figure (1904, pp. 255-256, fig. 1), the postero-ventro-lateral plates are of a peculiar type. However, it should be noted that Eastman had only the ventral laminae, and that their margins were incomplete posteriorly. In two incomplete specimens from Endlich Mesa (PF 354, PF 361) the postero-ventro-laterals agree closely with those of *B. canadensis*.

Pectoral appendages: As has been pointed out above, the type of *B. coloradensis* undoubtedly possessed a jointed pectoral fin, divided into proximal and distal segments. The specimen figured by Eastman from Endlich Mesa (1904, fig. 4; U.S.N.M. no. 16853) is part of the proximal segment of a very large individual, the preserved part measuring 98 mm. in length. Its narrow appearance is due to the fact that the margins are missing. A specimen that I collected (PF 355, fig. 39, A) shows a crushed proximal segment, with the proximal articulation preserved but the distal articulation missing; its estimated length was 78 mm. One of the specimens in the United States National Museum collected at Rockwood shows the distal segment of the appendage, but it is too poorly preserved to furnish any distinctive characters.

Comparison with other species: The study of the new material and restudy of the old collections from southwestern Colorado show that *Bothriolepis coloradensis* is similar in many respects to *E. canadensis* and *B. cellulosa*. It differs from both in the shorter,

¹ Measurements as in Stensiö, 1948, pp. 11-16.

broader levator fossa of the antero-median-dorsal plate, with the post-levator crests approaching in front of the anterior ventral pit, in the narrower anterior border of the antero-median-dorsal plate, and in the broader dorsal lamina and straighter anterior ornamented border of the mixilateral plate. It resembles *B. cellulosa* but may be distinguished from *B. canadensis* in its reticular and ridged type of adult ornamentation. *B. canadensis*, known only from the Late Devonian of Quebec, is clearly distinct from *B. coloradensis*. Better material of *B. coloradensis* will probably show additional differences from *B. cellulosa*; it is hardly likely that the two are cospecific, since *B. cellulosa* occurs in the Baltic States, northwestern Russia and Siberia (Gross, 1941a; Stensiö, 1948).

Other species of *Bothriolepis* reported from North America include *B. traquairi* Bryant, *B. minor* Newberry, and *B. nitida* (Leidy). *B. traquairi* from Quebec is so distinct in its ventral trunk armor that it may not belong to this genus (Bryant, 1924, p. 55; Stensiö, 1948, p. 400). *B. minor*, from the Late Devonian of New York and Pennsylvania, is inadequately described and defined. Its small size is not in itself distinctive, especially as Eastman (1899, p. 326) has referred to this species plates as big as those of *B. nitida*. Since the original description (Newberry, 1889, p. 112), it has been reported from the entire extent of the Late Devonian, and in two cases (Eastman, 1899; Willard, 1932, p. 29) from the same horizon and locality as *B. nitida*, so its geologic age cannot distinguish it from the latter. Its ornamentation, described by Newberry (1889, p. 112) as consisting of "fine, closely crowded vermicular furrows," only doubtfully distinguishes it from *B. nitida*. *B. nitida* has never been adequately described, although it occurs abundantly in the Late Devonian rocks of northern Pennsylvania and southeastern New York. The type is a distal segment of a pectoral fin from Tioga County, Pennsylvania, originally described (Leidy, 1856a, p. 11) as an "ichthyodorulite." Additional material has been described since that time by Newberry (1889, p. 111, pl. 18, fig. 2; pl. 20, figs. 1-5) as *B. "leidyi,"* and by Eastman (1907, pp. 50-51, pl. 3, fig. 4; pl. 7, fig. 1) as *B. nitida*, but their accounts do not allow a satisfactory diagnosis to be made. I have briefly examined material of this species from Tioga County, Pennsylvania, collected by Andrew Sherwood and R. H. Lacoe, and now in the United States National Museum. The material does not permit a complete diagnosis to be made, but clears up important points regarding the structure of *B. nitida*.

The size attained is quite considerable; one antero-median-dorsal plate in the United States National Museum collection measures

62.5 mm. in length, comparable to a large *B. canadensis*. The ornamentation, even in large, fully mature plates, retains some reticular character, although in places the reticulations are broken into tubercles or sinuous ridges. The ornamentation of the distal segment of the pectoral fin (U.S.N.M. no. 1982) is not strictly linear as shown by Leidy (1856b, pl. 16, figs. 7, 8), Cope (1891, pl. 30, fig. 7) and Eastman (1907, pl. 3, fig. 4), but is elongate reticular. The centro-nuchal plate is incompletely known, but is distinguished from *B. canadensis* by an important character. The posterior oblique cephalic pit lines come together rather far forward, and at their point of approach are separated by a wide ornamented area from the smooth nuchal area forming the posterior edge of the plate. This same feature is found in *B. cellulosa*, *B. panderi*, and *B. minor*, as well as in *Bothriolepis* from Colorado and Wyoming, as will be seen below. The antero-median-dorsal plate agrees in general with that of *B. canadensis*, but, as in the case of *B. coloradensis*, the post-levator crests approach each other in front of the anterior ventral pit, resulting in a relatively short, broad levator fossa. No characters have been found that would distinguish the postero-median-dorsal plate from that of *B. canadensis*. The antero-dorsal-lateral has a relatively wide dorsal lamina, the ratio of its length/width being 2.1. The antero-ventro-lateral plate also has a rather broad ventral lamina, the ratio of its length to its width being 2.1; it is not as broad as Stensiö (1948, p. 396) estimated from Newberry's figure of an incomplete plate. The postero-ventro-lateral plate indicates that this species had relatively high lateral walls in its trunk shield; the length/height ratio is 2.1, about as in *B. canadensis*. The postero-ventro-lateral also has a rounded dorsal corner as in the latter species, and probably in *B. coloradensis*. The pectoral fin is more slender than in *B. canadensis* of equal size. The ratio of length/width of the proximal segment in the large individuals measured is 5.2, while in *B. canadensis* of comparable size it is 3.3 to 3.6. In the distal segment the length/width ratio is 5.2 to 5.4 in large *B. nitida*, 4.0 to 4.8 in large *B. canadensis* (ratios computed from measurements of figures in Stensiö, 1948).

It is interesting to note in reviewing these characters of *B. nitida* that it cannot be clearly distinguished from *B. coloradensis*. It is possible that these two species will be found to be identical, in which case *B. nitida* must have priority. Before the question can be settled, more specimens of *B. coloradensis* are needed, and a restudy of all the *Bothriolepis* material from New York and Pennsylvania is desirable. In the meantime, *B. coloradensis* is retained provisionally.

Other occurrences of *Bothriolepis coloradensis*: Fragments of *Bothriolepis* have been collected by Walcott (1880, p. 225) and Noble (1922, p. 52) from the base of the Temple Butte formation in Lower Kanab Canyon and Grand Canyon, Arizona. The remains are not sufficiently well preserved to permit specific identification, but the reticular, non-tubercular type of ornamentation on plates of rather large size suggests that they may belong to *B. coloradensis*. In light of the comparisons made above, it is interesting to note that these were identified by Gidley (Schuchert, 1918, p. 361) as *B. nitidens* (=*B. nitida*), and by Eastman (United States National Museum collection) as *B. leidyi* (=*B. nitida*).

A few fragments in the United States National Museum, collected near Glenwood Springs, Garfield County, Colorado, also resemble *B. coloradensis* in their ornamentation. According to their label they came from the formation overlying the Cambrian shales and are presumably from the Parting member of the Chaffee formation.

In 1913, Cockerell reported fossil fishes from the cirque above Boulder Lake at the north end of Fossil Ridge, Gunnison County, Colorado. Since Cockerell did not give specific localities for the different fishes he described, it is not possible to compare his identifications with those made later. Kirk (1930, 1931) showed that Cockerell's specimens came from the Devonian, not the Ordovician, and Bryant and Johnson (1936) reported crossopterygians from the Parting member of the Chaffee formation at this locality. In the summer of 1949, I visited this site and collected from the Parting member not only crossopterygian remains, but fragments of a large *Bothriolepis*. The few plates obtained do not allow an entirely satisfactory comparison, but it is probable that they belong to *B. coloradensis*. The ornamentation of young individuals is apparently reticular, as is usual in this genus. On large mature individuals much of this reticular character is retained but with development of sinuous ridges in certain regions, exactly as in *B. coloradensis*. One unidentified fragment of a very large individual (PF 587) has the ridged character developed over part of its extent to a very high degree (fig. 40, C). The fossil "with vermicular ridges" ascribed by Cockerell to *Rhizodus* is probably such a fragment of *Bothriolepis*. The size attained by these central Colorado *Bothriolepis* was perhaps even greater than that recorded for *B. canadensis* and the typical *B. coloradensis*. The total length of a centro-nuchal plate (measured as in Stensiö, 1948, fig. 1) is approximately 37 mm. and its para-median length is 34 mm. (PF 591). The postero-median-dorsal and

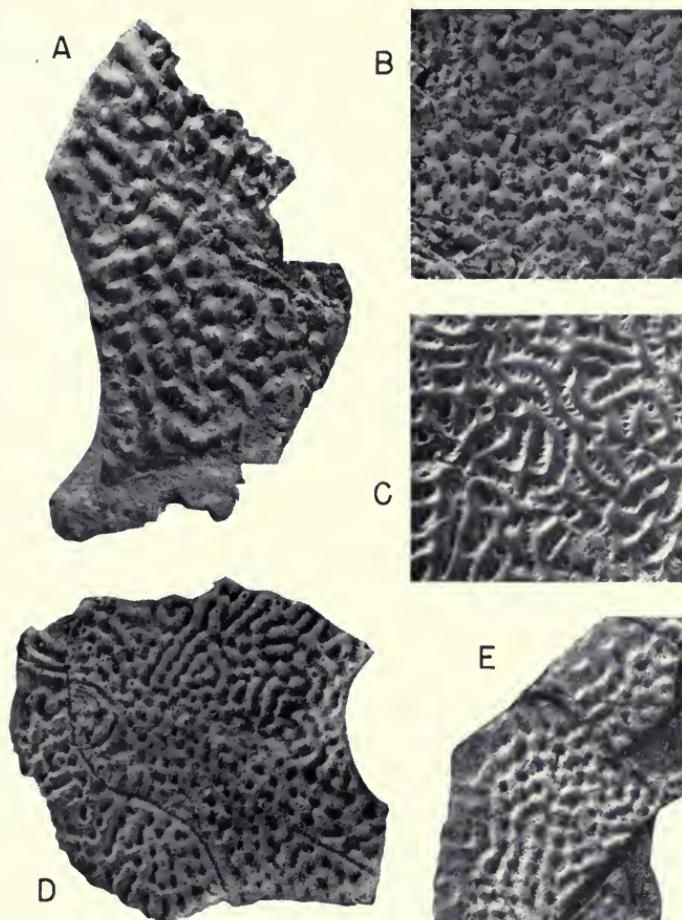


FIG. 40. *Bothriolepis*, dermal bone ornament ($\times \frac{3}{2}$). A, B. *B. darbiensis*, sp. nov., left half of centro-nuchal plate, Univ. Mich. 27547, Teton Pass, Wyoming. B. *B. darbiensis*, sp. nov., undetermined plate of large individual, PF 378, near Fort Washakie, Wyoming. C, *B. coloradensis*(?), undetermined plate of large individual, PF 587, Fossil Ridge, Gunnison County, Colorado. D, *B. coloradensis* Eastman, cast of impression of left lateral plate, PF 364, Endlich Mesa, La Plata County, Colorado. E, *B. coloradensis*, part of postero-median-dorsal plate, PF 362, near Columbine Lake, La Plata County, Colorado.

postero-median-ventral plates agree with those of *B. coloradensis*. A ventral central plate (Cv_1), measuring 81 mm. in length and thus of a large individual, indicates a pectoral fin of about the same proportions as in *B. canadensis*; the ratio of length/width is 2.8 (fig. 38, C). The centro-nuchal, unknown in *B. coloradensis* from southwestern Colorado, is represented by three, more or less complete,

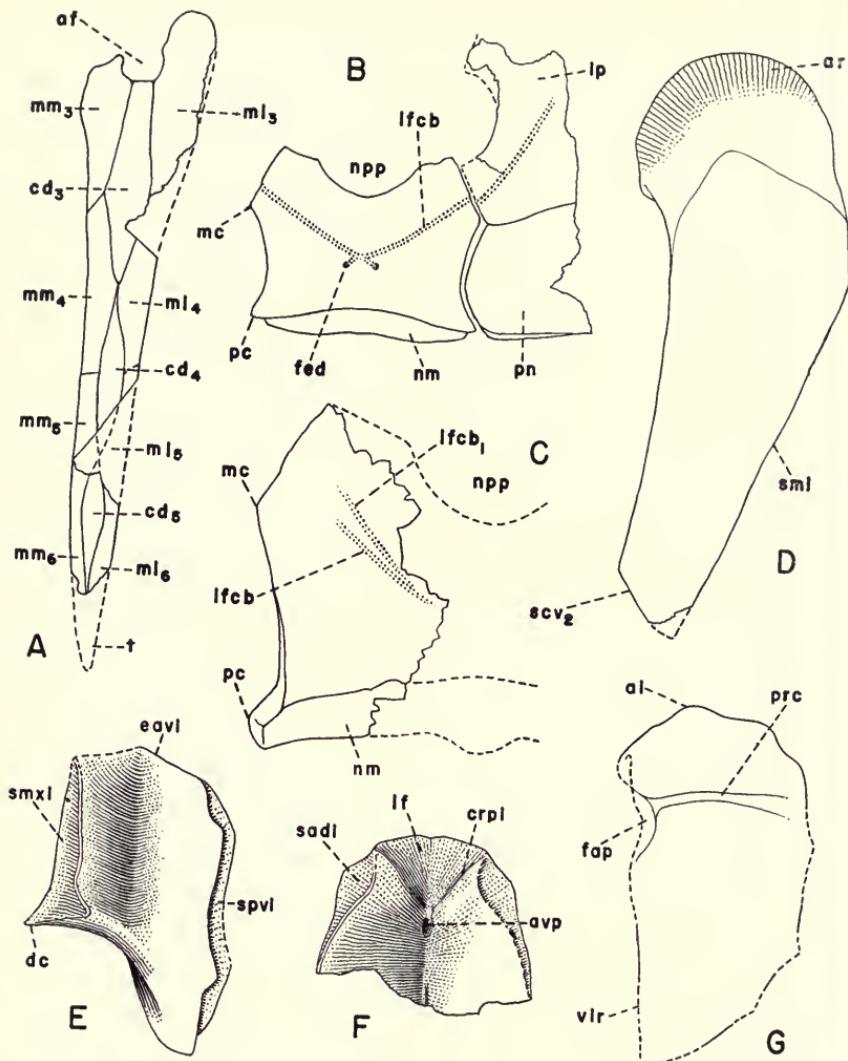


FIG. 41. *Bothriolepis darbiensis*, sp. nov. (B, $\times 2$; A, C-G, natural size).
 A, Distal segment of right pectoral fin, dorsal side, Univ. Mich. 27546. B, Type, centro-nuchal and incomplete right paranuchal and lateral plates, PF 396. C, Left half of centro-nuchal plate, Univ. Mich. 27547. D, Right ventral central plate, based on PF 366 and PF 365. E, Left postero-ventro-lateral plate, inner side, based largely on PF 396. F, Antero-median-dorsal plate, anterior half, inner side, PF 407. G, Right antero-ventro-lateral plate, ventral lamina, PF 381. A and C from Darby formation, Teton Pass, Wyoming; B, D-G, from Darby formation, near Fort Washakie, Wyoming. af, articular fovea; al, antero-lateral corner; ar, articular area; avp, anterior ventral pit; cd₃₋₅, dorsal central plates; crpl, post-levator crest; dc, dorsal corner of postero-ventro-lateral plate; eavl, eav; ip, lateral plate; lfc, centro-nuchal and incomplete right paranuchal and lateral plates; lfcbl, left half of centro-nuchal plate; lfcbr, right ventral central plate; mc, centro-nuchal plate; npp, postero-ventro-lateral plate; pn, lateral plate; scvg, right antero-ventro-lateral plate; smi, ventral central plate; smxl, postero-ventro-lateral plate; spvl, postero-ventro-lateral plate; vir, ventral lamina.

(Continued on page 233)

large specimens, and shows some interesting features (fig. 38, A). The postero-median process is strong, and the postero-lateral corners are very long and pointed, comparable to the situation in *B. maxima* (Gross in Stensiö, 1948, figs. 236, 237). This may not be too reliable a specific character, since it probably is correlated to some extent with the large size of these individuals; in *B. canadensis*, these processes and corners become more pronounced with increasing age (Stensiö, 1948, fig. 93). A characteristic of greater taxonomic value is the relatively very short anterior part of the lateral margin; the ratio of the anterior to the posterior part of this margin is 0.39 compared to 0.70–0.85 in *B. canadensis*. Of significance also is the fact that the posterior oblique cephalic pit lines meet relatively far forward, and are separated by a wide ornamented strip from the nuchal area, exactly as in *B. nitida*.

Bothriolepis darbiensis,¹ sp. nov.

Type.—C.N.H.M.—PF 396, a centro-nuchal plate with part of the right paranuchal and right lateral plates attached, belonging to a small individual (fig. 41, B).

Type locality.—Late Devonian, Darby formation, SW. $\frac{1}{4}$, sec. 18, T. 1 S., R. 2 W., on South Fork of Little Wind River, near Fort Washakie, Wind River Indian Reservation, Wyoming.

Diagnosis.—A species of *Bothriolepis* attaining about the same size as *B. canadensis* and *B. coloradensis*. Ornament of small individuals reticular, with slight tubercular elevations at junctions of ridges; ornament of large individuals consisting of tubercles and nodose, sometimes sinuous, ridges, often with a somewhat concentric disposition near the borders of trunk plates (fig. 40, A, B). Posterior oblique cephalic pit lines coming together about half way between the post-pineal notch and the posterior border of the centro-nuchal

edge overlapped by antero-ventro-lateral plate; *fap*, articular fossa for pectoral fin; *fed*, external opening of endolymphatic duct; *ifcb*, posterior oblique cephalic pit line; *ifcb₁*, anterior oblique cephalic pit line; *lf*, levator fossa; *lp*, lateral plate; *mc*, lateral corner between anterior and posterior divisions of lateral margin; *ml₃₋₆*, lateral marginal plates; *mm₃₋₆*, medial marginal plates; *nm*, unornamented nuchal area; *npp*, post-pineal notch; *pc*, postero-lateral corner of centro-nuchal plate; *pn*, paranuchal plate; *prc*, post-branchial crest; *sadl*, area overlapping antero-dorso-lateral plate; *scv₂*, suture for second ventral central plate; *sml*, suture for lateral marginal plate; *smx₁*, area overlapping mixilateral plate; *spv₁*, area overlapping right postero-ventro-lateral plate; *t*, terminal plate; *vlr*, ventro-atrial ridge.

¹ Named after the Darby formation of western Wyoming.

plate, with a wide ornamented border posterior to their junction (fig. 41, B, *ifcb*). Anterior part of lateral border of centro-nuchal plate about two-thirds as long as posterior part. The post-levator crests of the antero-median-dorsal plate approaching each other in front of the anterior ventral pit, resulting in a relatively short, broad levator fossa (fig. 41, F, *lf*). The lateral walls of the trunk shield relatively high, the ratio of length/height of the lateral lamina of the antero-dorsal-lateral plate being 2.0-2.4, of the mixilateral 2.9-3.0. The angle between the dorsal and lateral walls of the trunk shield probably relatively great (120°-125°) resulting in a high trunk shield. The antero-dorsal-lateral plate with a weak post-nuchal corner, and the antero-ventro-lateral plate with a weak antero-lateral corner (fig. 41, G, *al*). The lateral lamina of the postero-ventro-lateral plate with a pronounced pointed dorsal corner (fig. 41, E, *dc*). Pectoral fin more slender than in *B. canadensis* of comparable size; the ratio of length/width of ventral central plate (Cv_1) is approximately 3.7 in small and 3.2 in large individuals (fig. 41, D).

Discussion.—Fish remains were first discovered on the South Fork of the Little Wind River by N. H. Brown of Lander, Wyoming. These fragmentary fossils from the Darby formation were first identified as *Dinichthys* and *Acanthaspis* (Branson, 1929), then as "a new genus of fishes closely allied to *Pterichthys*" as well as some fishes of Early Devonian affinities (Branson and Mehl, 1930), and finally as "ostracoderms" (Branson and Branson, 1941). In 1949, I was able to collect at this site and obtained, with the exception of a few remains of crossopterygians, only plates and fragments of *Bothriolepis darbiensis*. There can be no question of their Late Devonian age.

Most of the material collected in 1949 consists of isolated plates of small, presumably juvenile individuals. Remains of larger individuals are common, but are difficult to collect because of the nature of the matrix and poor preservation of the bone. Because of the individual age difference of the majority of the available specimens, comparison with *B. coloradensis* is difficult, but it is apparent from the diagnosis above that the two species are similar in many respects and presumably closely related. *B. darbiensis* may be distinguished from *B. coloradensis* and *B. nitida* by its more tubercular type of adult ornamentation (fig. 40, A, B), by the longer anterior part of the lateral border of the centro-nuchal plate (fig. 41, B), by the weak development of the antero-lateral process of the antero-ventro-lateral plate (fig. 41, G), and by the pronounced pointed dorsal corner

of the postero-ventro-lateral plate (fig. 41, E, *dc*). More material would undoubtedly reveal additional differences. From *B. canadensis*, which it resembles in ornamentation, it may be distinguished by the more anterior meeting of the posterior oblique cephalic pit lines on the centro-nuchal plate (fig. 41, B, *ifcb*), by the relatively short, broad levator fossa on the antero-median-dorsal (fig. 41, F, *lf*), by the weaker post-nuchal corner of the antero-dorso-lateral, and the weaker antero-lateral corner of the antero-ventro-lateral (fig. 41, G, *al*), by the probable higher angle between the dorsal and lateral walls of the trunk shield, by the pronounced dorsal corner of the postero-ventro-lateral (fig. 41, E, *dc*), and by the more slender pectoral fins (fig. 41, D).

In 1947, Foster reported the discovery of fish remains in the Leigh member of the Bighorn formation on Glory Mountain, near Teton Pass, Teton County, Wyoming. J. T. Gregory considered the fish to be arthrodire and probably Devonian in age. Through the kindness of Dr. Claude W. Hibbard of the University of Michigan, I have been able to examine this material, and find that it consists almost entirely of fragmentary remains ascribable to *Bothriolepis darbiensis*. Since the Leigh member is Late Ordovician in age, it is apparent that the formation has been misidentified, and the thin-bedded sandy limestones that contain the fish should be referred to the lower part of the Darby formation of Late Devonian age.

The available identifiable plates from Teton Pass are few, and are all of very large individuals, exceeding in size any individuals of *B. canadensis*, *B. coloradensis*, or *B. darbiensis* that I have measured. A distal segment of the pectoral fin (Univ. Mich. 27546) measures 75 mm. in length, excluding the anconeal processes. A centro-nuchal (Univ. Mich. 27547) has an estimated paramedian length of 45 mm. The ornamentation is distinctly tuberculate, although the tubercles are in places united more or less into short ridges (fig. 40, A). The centro-nuchal (Univ. Mich. 27547) agrees with that of *B. darbiensis* in the proportions of the anterior and posterior parts of the lateral margin (figs. 40, A; 41, C) and in the position of the posterior oblique cephalic pit lines; its postero-lateral corners are moderately large, but blunt (fig. 41, C, *pc*), and not produced into sharp points as in large *B. coloradensis*. The antero-ventro-lateral (Univ. Mich. 27548) agrees with that of *B. darbiensis* in having a reduced antero-lateral process. The pectoral fin is relatively slender, the distal segment of the very large individual having a ratio of length/width of 5.0 (fig. 41, A).

ARTHRODIRA

Arthrodires have been reported from the Late Devonian in many places in the western United States. They are definitely present in large numbers in the near shore facies of the Jerome formation of Arizona, but most of the other records in the Rocky Mountain region are open to question. Eastman (1904, p. 258) mentioned, but did not figure, "a finely tuberculated plate . . . which appears to be a posterior ventral of some Arthrodire, of about twice the size of the type species of *Coccosteus*." This plate was collected from the Elbert formation on Little Cascade Creek, about one-half mile south of Columbine Lake, La Plata County, Colorado. In 1949, at this locality, I collected crossopterygian remains showing a fine tuberculation, and I venture to suggest that Eastman's specimen may belong to the same form. Cockerell (1913, p. 246) reported a plate resembling *Coccosteus*, having a structure nearly identical with *Astraspis*, from what is presumably the Parting member of the Chaffee formation in Gunnison County, Colorado. I have not seen this specimen, nor is it possible from Cockerell's description to determine the exact locality, but it is probable that he misidentified the plate; no arthrodires have been reported from this region by subsequent collectors.

Eastman (1904, pp. 258-259) rather doubtfully assigned to arthrodires some finely tuberculated plates from the Parting Quartzite, near Aspen, Pitkin County, Colorado. The only determinable specimens in my own collection from Aspen belong to a crossopterygian; its plates and scales are often finely tuberculated, and it is possible that this is the form that Eastman identified as arthrodiran. Bryant (Bryant and Johnson, 1936, p. 658) recognized two types of arthrodires, resembling *Aspidichthys* and *Dinichthys*, in the Parting member of the Chaffee formation on Gribbles Creek, Fremont County, Colorado. Only fragments were available to Bryant, but his identification was supported by thin sections and may be considered as probably correct. The "*Dinichthys*" and "*Acanthaspis*" that Branson reported (1929) from the Darby formation near Lander, Wyoming, are undoubtedly specimens of *Bothriolepis darbiensis*. According to Newton Brown of Lander (personal communication), they were collected from the same locality as the type of the latter species.

I have been unable to obtain for study the "arthrodire jaw" reported by Baker (1946, p. 575) from Sheep Mountain on the southwest side of the Wind River Mountains.

DIPNOI

Lung fishes are not uncommon in Late Devonian formations of the western United States, but, with the exception of a few questionable scales, only dental plates have been recognized. Unfortunately, it is becoming increasingly evident that a single tooth or a few teeth are insufficient to diagnose a species. There are numerous cases where several species, described from a small collection of dental plates, have been shown to be variations of a single species when a large series of plates has become available. Thus, Miall (1878, p. 27), with 350 *Ceratodus* teeth to study, was able to reduce to only two the many species described by Agassiz from the Rhaetic of Aust Cliff, near Bristol, England. Peyer (Stromer and Peyer, 1917, p. 61) concluded that many of the species previously described from the Triassic of Europe were synonyms. The variation of dental plates within a single species can be great, as is well shown by Peyer (1924, pl. 1) in *Ceratodus africanus* Haug, and is due to a number of factors. Because lung fish dental plates can grow, even while functional (Stromer and Peyer, 1917, pp. 46-48), there may be considerable difference in their size in juvenile and old individuals; within a single species, *Ceratodus africanus*, the length of the dental plate may range between 13 and 77 mm. (measurements from Peyer, 1924, pl. 1). Palatal and splenial tooth plates differ, and an isolated plate is often difficult to place. Wear may greatly change the appearance of teeth in old individuals, and finally post-mortem erosion, even possibly by digestive fluids of predators (Eastman, 1908, p. 217), must be considered. Taking all these facts into consideration, minor differences exhibited by a single specimen or a small sample are not necessarily valid criteria for the erection of a new species.

Among the species of *Dipterus* described from the Devonian of North America, two from the Middle Devonian resemble each other in having only a few rows of compressed denticles (each denticle presumably representing a tooth ontogenetically) fused only at the base. The unique tooth of *D. eastmani* Stauffer from Ohio was distinguished from *D. uddeni* Eastman of Iowa because it had one less major ridge of denticles; but Stauffer's figures suggest that the inner ridge in his specimen may have been reduced by wear. *D. sherwoodi*, from the "Catskill group" of Pennsylvania is of a similar type. Eastman (1908, p. 214) came to the conclusion that a number of species from the Late Devonian of New York and Pennsylvania were variants of *D. nelsoni* Newberry; he showed that *D. flabelliformis* represented palatal tooth plates, *D. levis* a worn tooth plate,

and *D. quadratus* and *D. minutus* juvenile specimens. All are characterized by numerous (9 or 10) ridges with the denticles fused except at the tips. Another group of four species from the Late Devonian is characterized by having from six to eight ridges composed of denticles that are rounded in cross section (or perhaps somewhat compressed on the medial side of the plate) and fused only at the base. Two of these, *D. mordax* and *D. pectinatus*, from the State Quarry beds of Iowa, were recognized as being closely similar by their describer (Eastman, 1908, p. 223). Other species having this type of dental plate are *D. gemmatus* Hussakof and Bryant from the Genesee group of New York State and *D. johnsoni* Bryant from the Chaffee formation of Colorado. It is possible that *D. fleischeri* Newberry, from the "Catskill group" of New York and Pennsylvania, is related to this group. At present there are no entirely satisfactory characters to distinguish these species. A number of the Late Devonian teeth from the Rocky Mountain region belong to this type and are discussed below:

Dipterus mordax Eastman: The first definite record of Late Devonian lung fish in the western United States was a small collection of dental plates described by Eastman (1915, p. 282) from the Elbert formation, La Plata County, Colorado. One of these (op. cit., fig. 3) was identified as a juvenile *D. mordax*, another (op. cit., fig. 4) as *D. pectinatus*. In my opinion the former, with its relatively narrow proportions and convex functional surface, may represent a splenial tooth, and the latter, with its broader proportions (although not as restored), may be a palatal tooth of the same species, *D. mordax*. An incomplete tooth collected in the same region in 1949 (PF 583) is probably also referable to *D. mordax*.

In 1936, Bryant (Bryant and Johnson, 1936, pp. 658-659) described *D. johnsoni* from the Parting member of the Chaffee formation in two localities in central Colorado. This species agrees very closely with *D. mordax*, to which it probably belongs.

Species based on worn dental plates: A number of North American species of *Dipterus* have been based on what are presumably worn dental plates. It is possible that they belong to some of the species mentioned above, but without a series including intergrading forms, their exact relationship must remain uncertain. *D. contraversus* from the "Catskill group" of Pennsylvania is such a type. Another is *D. calvini*, which does not seem to be related to *D. uddeni*, associated with it in the Cedar Valley limestone of Iowa. *D. costatus*, from the State Quarry beds of Iowa, appears to have more compressed

denticles than the *D. mordax*-*D. pectinatus* group in the same formation. The teeth from the State Quarry beds referred to *D. digitatus* have much of the functional surface smooth, with a tumid ridge on the inner margin, features suggestive of worn tooth plates. Some of the tooth plates of this species figured by Eastman (1908, pl. 7, figs. 16-25) have the distal part of the ridges only slightly worn, with the individual denticles clearly distinct; others have the ridges more completely worn, shorter, and with the denticles hardly discernible. There is no great gap between the latter and the dental plates figured by Eastman (op. cit., pl. 8) as *Conchodus variabilis*. Considering the differences between young and worn teeth demonstrated in *Ceratodus parvus* (Stromer and Peyer, 1917, pp. 26-32), and *C. africanus* (Peyer, 1924, pl. 1), it seems very probable that *Conchodus variabilis* Eastman represents dental plates of *Dipterus digitatus* showing even greater wear. Many of the dental plates of *D. digitatus* figured by Eastman (op. cit., pl. 7, figs. 20, 22, 24) are suggestive of *D. mordax* in having discrete denticles, roundish in section. Their relationship to the latter species, however, cannot be demonstrated from the figures.

Dipterus digitatus has been recorded in the Early Mississippian, Bushberg sandstone of Missouri and is known from the Late Devonian of the Rocky Mountain region as well. A greatly worn tooth from the Elbert formation of southwestern Colorado (Eastman, 1915, fig. 2) was identified as *D. digitatus*; it could conceivably belong to an old individual of *D. mordax*. An incomplete and highly worn tooth of this type in the University of Michigan collection (no. 27549) was collected in the Darby formation near Teton Pass, Teton County, Wyoming. The functional surface is flat or slightly concave, and the ridges are short and low, with only a suggestion of the original denticles. Another tooth showing a superficial resemblance to *D. digitatus* was collected in 1950 by Bryan Patterson, 108 feet above the base of the Jefferson formation, in Blacksmith Fork Canyon, Bear River Range, Utah (PF 495). It resembles *D. digitatus* in having nearly two-thirds of the functional area worn smooth, and in having an inner tumid ridge. From its narrow proportions and convex functional surface it is probably a splenial tooth plate. Its length is only 9 mm. and a worn tooth is hardly to be expected in such a small individual of *D. mordax* or *D. digitatus*. This may well represent a distinct species, but is hardly definable from a single worn specimen.

Other records of Dipnoi: Undescribed and unidentified *Dipterus* dental plates have been reported from the Jefferson formation near

Logan, Montana (Eastman, 1917, p. 246) and from the Jerome formation, near Flagstaff, Arizona (Hussakof, 1942, p. 9).

A new species of *Conchodus*, *C. parvulus*, was described by Bryant (Bryant and Johnson, 1936, p. 659) from the Parting member of the Chaffee formation at Cross Mountain, Gunnison County, Colorado. This is the third species referred to this genus in North America. The first, *C. plicatus* Dawson, from the Coal Measures of Nova Scotia, was believed by Woodward (1891, p. 255) to represent an "abraded dental plate of *Ctenodus*." The second, *C. variabilis* Eastman, from the Late Devonian of Iowa, intergrades with *Dipterus* teeth, as Eastman himself recognized (1898, p. 113); as was suggested above, it probably is founded on worn teeth of *Dipterus*. Bryant's species, *C. parvulus*, may also represent worn teeth of *Dipterus johnsoni* (= *D. mordax*), which is found in the same formations at the same locality.

The genus *Synthetodus* was considered by Eastman (1898, pp. 112-113; 1908, p. 231) to represent dental plates of Dipnoi, but this was questioned by Hussakof and Bryant (1919, p. 151), who provisionally referred it to the Cochliodontidae. Whatever the relationships of *Synthetodus*, the partial plate from the Elbert formation of southwestern Colorado, figured by Eastman (1915, fig. 1), shows little resemblance to the type material from the Late Devonian of Iowa. Probably it is the pavement tooth of one of the Bradyodonti.

CROSSOPTERYGII

HOLOPTYCHIIDAE

Holoptychius cf. *giganteus* Agassiz: Eastman (1904, pp. 257-258) reported two species of *Holoptychius* from the Elbert formation of Endlich Mesa, La Plata County, Colorado. His identification was based upon scales alone, those having an ornamentation of irregular, tortuous ridges being referred to *H. giganteus* Agassiz, and those ornamented with tubercles to *H. tuberculatus* Newberry. Scales from the same horizon and locality in Chicago Natural History Museum resemble those described by Eastman. They demonstrate that the ridged and tuberculated types of scale form an intergrading series, and that both fall within the limits of *H. giganteus* as defined by Agassiz (1845, pl. 24, figs. 3-10). There is little reason to believe that two species are present in the same bed at this restricted locality, especially when they are distinguished only by scales, which are hardly sufficient to define a species of this genus satisfactorily. No

character is known by which the Elbert formation scales may be distinguished from those of *H. giganteus*, although if more complete remains were available, the Colorado *Holoptychius* would probably prove to be specifically distinct.

Other specimens obtained from the same locality and horizon include a natural cast of a lower jaw fragment, the impression of the inner side of the anterior part of the skull roof, as well as some impressions of deeply ornamented dermal bone fragments. Presumably all belong to *Holoptychius*.

Holoptychius sp.: There are two published records of crossopterygians from Fossil Ridge, Gunnison County, Colorado. Cockerell (1913, p. 246) mentioned a fragment covered with vermiform ridges that he compared to *Rhizodus*, but his description suggests the ornament of *Bothriolepis coloradensis*. Bryant (Bryant and Johnson, 1936, p. 657) compared a crossopterygian from this locality to *Glyptopomus sayrei*. My collection from Fossil Ridge includes crossopterygian fragments, but only of *Holoptychius*. The scales resemble some of those from Endlich Mesa referred to *H. cf. giganteus*; the exposed part is ornamented with wavy, branching ridges, but no tubercles. The teeth clearly belong to the Holoptychiidae. The fang teeth are slightly curved, flattened with two crests in the crown, and round in section without crests, but with many grooves in the lower part. The enamel is smooth on the crown, but has a number of sharp ridges between the grooves near the base. Thin sections are not satisfactory because of abundant burrows attributed to fungi, called *Mycelites ossifragus* (Peyer, 1945). It is possible, however, to determine that there are complex, branched dentine folds in the lower part of the teeth, and that enamel and cement do not enter the folds. The structure resembles that of *Holoptychius* and *Glyptopomus* as described by Bystrow (1939).

Scales from the Temple Butte formation in the Grand Canyon of Arizona were identified as belonging to *Holoptychius* by Gidley Schuchert, 1918, p. 361). They were not described, nor have I been able to find them in the collections of the United States National Museum.

RHIZODONTIDAE

*Litoptychus*¹ gen. nov.

Type species.—*Litoptychus bryanti* sp. nov.

¹ λιτός, simple + πτυχός, fold; in reference to the manner in which the dentine of the teeth is infolded.

Diagnosis.—Scales cycloidal, very thin, ornamented in exposed portion with wavy anastomosing ridges, and with a fan-shaped arrangement of rows of fine tubercles just anterior to the ridges. Fang teeth robust, oval in section, lacking trenchant edges, with furrows and grooves only in the lower half; dentine infolded mostly in very simple fashion at the base, with occasional simply branched

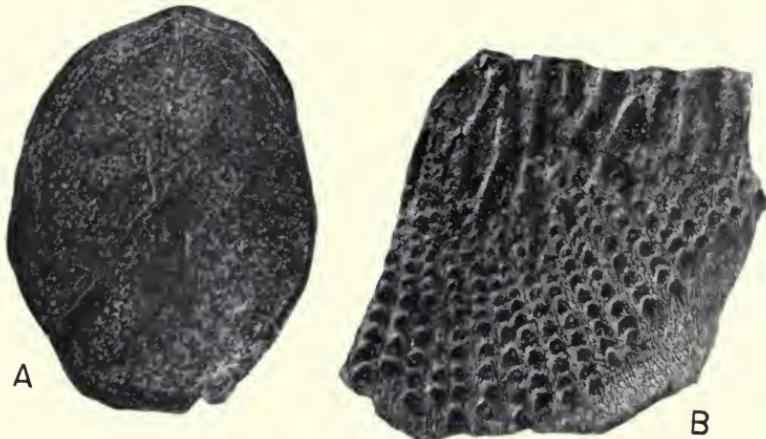


FIG. 42. *Litoptychus bryanti*, gen. and sp. nov. A, Inner side of scale, PF 619 ($\times 2$). B, Fragment of exposed area of scale, PF 617 ($\times 6$).

infoldings. Dermal bones mostly ornamented with tubercles united at least at the base by ridges. Dentary with internal expansion at anterior end of jaw overlying the symphysis and the prearticular; coronoids bearing large fang teeth, the dentary a small one. Vertebrae ring-shaped.

Litoptychus bryanti,¹ sp. nov.

Type.—C.N.H.M.—PF 610 (fig. 46), incomplete left lower jaw showing inner side, and preserving most of the dentary, intercoronoid and precoronoid, as well as parts of the prearticular and infradentalia.

Horizon.—Late Devonian. Lower member of the Chaffee formation (bed 29 of Johnson, 1944, pp. 362–363).

Locality.—Deadman's Creek, NW. $\frac{1}{4}$, sec. 23, T. 14 S., R. 84 W., Gunnison County, Colorado.

Diagnosis.—As for the genus. Scales as much as 30 mm. in diameter. Lower jaw attaining an estimated length of 210 mm.

¹ Named after the late W. L. Bryant, who gave the first description of Devonian fishes from central Colorado.

Discussion.—In 1936 Bryant (Bryant and Johnson, 1936, p. 657) reported the presence of a large crossopterygian in the lower member of the Chaffee formation on Deadman's Creek, Gunnison County, Colorado. A small collection from this locality in Chicago Natural History Museum consists mainly of fragments of a large fish that is surely the same one mentioned by Bryant. Apparently it belongs to the Rhizodontidae, and thus cannot be related closely to *Glyptopomus sayrei*, to which Bryant compared it. Nor can it be referred at present to any of the genera of Rhizodontidae hitherto described. It should be remarked, however, that many of the genera of this family are unsatisfactorily defined on the basis of tooth and scale characteristics, and until such time as a revision is undertaken the affinities of many members of this family must remain uncertain.

The scales of *Litoptychus bryanti* are large and cycloidal; those in the collection measure about 30 mm. in the antero-posterior diameter, and about 25 mm. in the shorter diameter. They are extremely thin, only about 0.25 mm. in thickness in the overlapped portion. The inner surface (fig. 42, A) shows a few faint concentric growth lines, especially near the periphery, and is marked with numerous pores; there is no central boss or ridge. The outer surface was not exposed on any of the specimens collected, and preparation was difficult because of their extreme thinness. The overlapped area of the scale is probably large and is marked with a very fine-meshed, elongated reticulation. Thin sections reveal that the surface here is composed of the middle or cancellar layer. Only one small fragment (PF 617) reveals the nature of the ornamentation of the exposed area of the scale (fig. 42, B). This consists of a fan-shaped arrangement of rows of very fine tubercles directed anteriorly, and a number of low ridges directed towards the posterior border; the ridges are wavy and anastomosing. In this ornament, they show some resemblance to *Strepsodus* (Woodward, 1891, pl. 16, fig. 1), to *Glyptolepis*, and perhaps to *Sauripterus* (Eastman, 1907, pl. 7, fig. 9). The tubercles and ridges of the scales are presumably composed of bone, not dentine, although thin sections through this part of the scale were not obtained. Most of the thickness of the scale is composed of the basal laminar layer, with the younger and deeper aminae obliquely overlapping the older, more superficial laminae near the periphery.

The fang teeth are robust, rapidly tapering, straight, and oval in section throughout their height. The upper half of the tooth has a smooth surface, while the lower half is marked with approximately

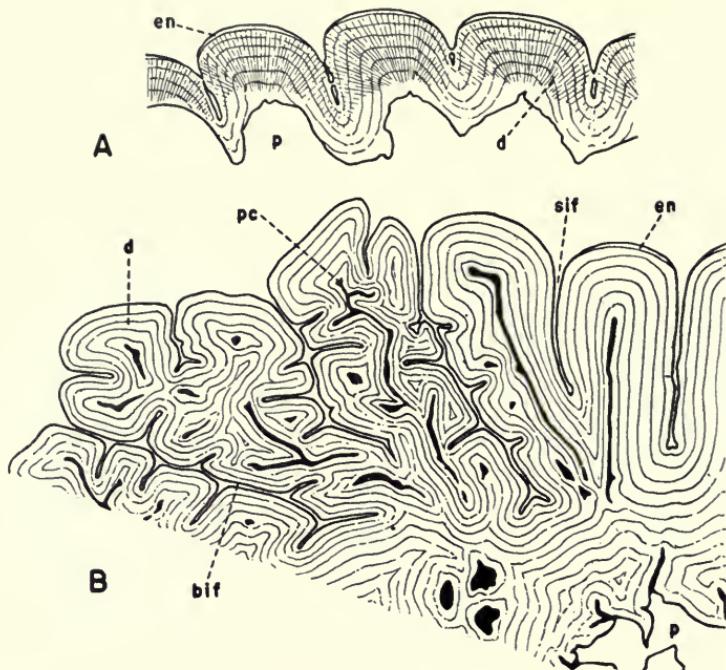


FIG. 43. *Litoptychus bryanti*, gen. and sp. nov. (× 25). A, Transverse section through base of fang tooth, PF 619. B, Obliquely transverse section through base of palatal fang, PF 616. *bif*, branched infolding of dentine; *d*, dentine; *en*, enamel; *p*, pulp cavity; *pc*, pulp canals; *sif*, simple infolding of dentine.

twenty deep furrows; the ridges between these furrows are occasionally marked by shorter, shallower grooves. These teeth show no fine ridges or trenchant edges. Cross sections of fang teeth indicate that the structure is relatively simple. One tooth (PF 619), approximately 7 mm. in maximum diameter, shows at the base only simple, open unbranched infoldings of the dentine; there is no indication of cement in the infoldings and enamel is restricted to the outer surface of the ridges (fig. 43, A). Another tooth (PF 616), 5.2 mm. in maximum diameter, has a number of large unbranched folds at the base, but on one side (the section is oblique, and this is presumably lower) there are simply branched infoldings (fig. 43, B). At mid-height there is no trace of any infolding, and the dentine tubules have a simple radial arrangement. The fang-tooth structure is much simpler than that described in *Eusthenopteron* and *Panderichthys (Polyptocodus)* (Bystrow, 1939).

The dermal bones of the skull and jaw are ornamented with rather small tubercles united near their bases, and sometimes to mid-height

or to the top (fig. 45). Superficially, the ornament resembles that of *Eusthenopteron*. An undetermined fragment (PF 618) has an elongate reticular ornament, similar to that figured by Gross (1936, fig. 1) on the pterygoids of *Porolepis* and *Panderichthys* (*Polyptodus*). In thin sections (fig. 44), the structure of the tubercles is not clear, presumably because of some peculiarity of preservation, but there is probably no dentine or enamel. The tubercles appear to be formed of bone of a lamellar type, as in *Eusthenopteron* (Byström, 1939, fig. 18, A). An expansion of the dentary near the symphysis bears true denticles composed of dentine and possibly enamel. Whether the prearticular bore similar denticles, as is the case in many crossopterygians, is not known. The dermal bones have a well-developed middle or cancellar layer and a thick basal laminated layer.

Three specimens of lower jaws are available, one (PF 613, fig. 45) showing a nearly complete outer surface, another (PF 610, fig. 46) the anterior two-thirds of the inner side, and the third (PF 619) the inner side of the external bones of the posterior part. PF 613 indicates a relatively deep jaw, the ratio of the depth at the inter-coronoid to the total length being 0.22. Its proportions agree quite well with those of the Holoptychiidae. The known Devonian Rhizodontidae have a more slender jaw, although some Carboniferous genera show a deepening. The considerable depth of the

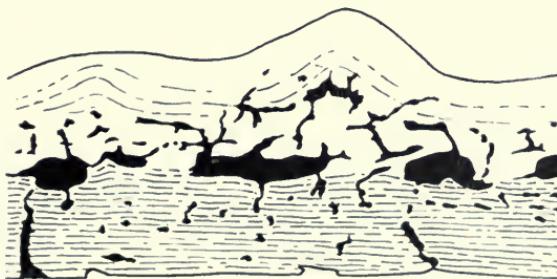


FIG. 44. *Litoptychus bryanti*, gen. and sp. nov. (X 25). Vertical section through dermal bone showing a thick basal laminated layer, a middle cancellar layer, and an upper layer consisting probably of laminated bone.

jaw is due to the deepening of the dentary anteriorly, as well as to an expansion of the infradentaries, especially the splenial.

The dentary shows a progressive feature; it is expanded horizontally in the symphysial region, where it comes to overlie the symphysis and the anterior end of the prearticular (fig. 46, dn_1).

In addition to the three large fang teeth borne by the coronoids, there is a small fang, 5 mm. in maximum diameter, in the dentary at the anterior end of the jaw (fig. 46, *df*). *Panderichthys* is the only other Devonian crossopterygian with dentary fangs (Gross, 1941b, figs. 18, 19); they are probably present in all the Late Paleozoic genera, certainly in *Rhizodus* and *Rhizodopsis* (Traquair, 1877, pp. 302-303) among the Rhizodontidae, and in *Ectosteorhachis* (= *Megalichthys*)



FIG. 45. *Litoptychus bryanti*, gen. and sp. nov. ($\times \frac{2}{3}$). Right lower jaw, PF 613, outer side.

Ag. 1844) among the Osteolepidae. The medial part of the dentary expansion that overlies the prearticular is covered with denticles, presumably composed of dentine and enamel.

Three coronoid bones are present, although the most posterior is not well shown in the available specimens. The first two, incompletely preserved in PF 610, bear larger fang teeth than does the dentary; the fang of the precoronoid is 11 mm. in diameter at the base, that of the intercoronoid 9 mm.

On the external surface (fig. 45) the sutures are poorly shown, only that between the dentary and infradentaries being partly discernible. At the level of the posterior fang tooth the dentary starts to deepen and in the anterior third of the jaw is very deep. This differs from the situation in *Holoptychius* and *Glyptolepis*, where the considerable depth of the anterior part of the jaw is due more to the expansion of the splenial, and the dentary remains relatively shallow.

A number of other fragmentary remains of *Litoptychus bryanti* are available. An operculum (PF 612), exposed on the inner side, agrees in general shape with that of *Eusthenopteron*. A parasphenoid (PF 614) is of the long narrow type characteristic of the Osteolepidae and Rhizodontidae. Fragments of the endocranum and of the dermal bones of the skull are present in the collection, but are not

sufficiently complete to offer any diagnostic characters. The vertebrae (PF 611, 619) have oval, ring-shaped centra with large notochordal foramina. There is no evidence of the paired lateral processes (?parapophyses) such as are present in *Strepsodus*, and no neural or haemal arches have been recognized. Scattered fin supports are common.

The relationship of *Litoptychus* to the Rhizodontidae is indicated by the simple manner in which the dentine of the fang teeth is infolded, and by the thin cycloidal scales. From *Eusthenopteron*, it may be distinguished by the presence of an anterior, fang-bearing expansion of the dentary, the greater depth of the lower jaw, the structure of the fang teeth, the ring vertebrae, and the scale ornamentation. *Tristichopterus* is closely related to *Eusthenopteron* and probably differs from *Litoptychus* in similar features. *Panderichthys* possesses a dentary fang, but has a very peculiar and distinctive tooth structure, and rhombic scales set with tubercles. *Sauripterus* is insufficiently known. It may resemble *Litoptychus* in its scales and dermal bone sculpture, but it differs in having a shallow jaw and fang teeth with trenchant edges. *Rhizodus* is characterized particularly by its fang teeth, which possess one or two sharp trenchant edges. The dentary fang is much larger than the coronoid fangs in the jaw figured by Woodward (1891, pl. 12, fig. 1). In *Rhizodopsis*, the teeth lack the cutting edges and the scales are very

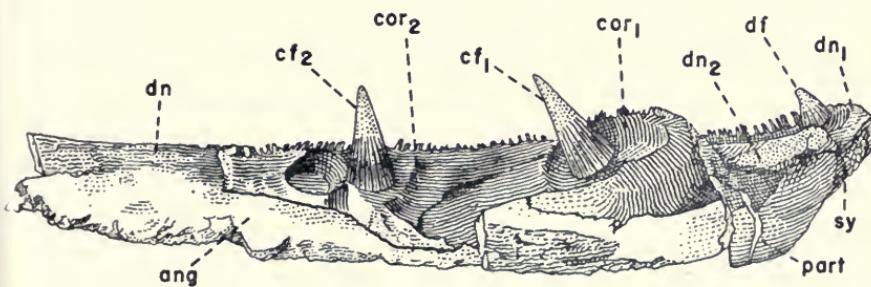


FIG. 46. *Litoptychus bryanti*, gen. and sp. nov. (X 2/3). Type, PF 610, incomplete left lower jaw, inner side. *ang*, angular; *cf₁*, *cf₂*, coronoid fangs; *cor₁*, precoronoid; *cor₂*, intercoronoid; *df*, dentary fang; *dn*, dentary; *dn₂*, denticulate expansion of dentary overlying prearticular; *part*, prearticular; *sy*, symphysis.

thin as in *Litoptychus*, but the scales are typically of a narrow ovoid shape and the dentary fang is apparently larger than those borne by the coronoids, as in *Rhizodus*. *Strepsodus* is incompletely known and

is characterized at present chiefly by its slenderly tapering teeth with a peculiar curvature.

Litoptychus cannot be assigned to any of the previously described rhizodontid genera as they are now defined. It is clearly a rather progressive genus for the Devonian, showing many features in common with the Carboniferous members of the family.

OSTEOLEPIDAE

In addition to the common, large rhizodontid in the Chaffee formation at Deadman's Creek, Gunnison County, Colorado, there

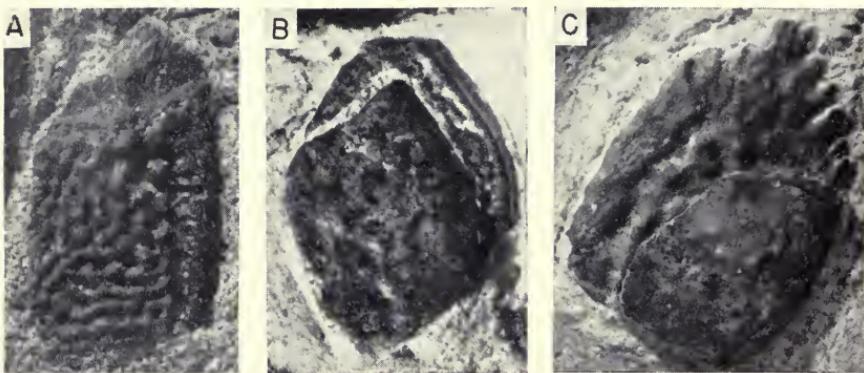


FIG. 47. Osteolepidae indet., from Parting member of Chaffee formation, Colorado. A, Tuberculate scale, PF 603 ($\times 4$), Spar Gulch, near Aspen. B, Smooth scale, PF 599 ($\times 9$). C, Scale with superficial layer partly covering exposed area, PF 598 ($\times 4$). B and C from Deadman's Creek, Gunnison County, Colorado.

are occasional scales and dermal plate fragments of a small fish belonging to the Osteolepidae. The scales have a rhombic exposed area, 4.0–7.5 mm. in length, covered with a smooth superficial layer of dentine and enamel (fig. 47, B). The overlapped area is relatively narrow and is separated from the exposed area by a narrow groove. The inner side has a central longitudinal ridge or boss. A thin section shows the typical osteolepid structure, with a well-developed laminated basal layer, a middle cancellar layer that forms the surface of the overlapped area, and in the exposed area a thin superficial layer with the usual flat-topped denticles of dentine and enamel. Many details of the structure are obscure because of the abundance of borings attributed to fungi (*Mycelites ossifragus*). The dermal plate fragments are usually completely covered with dentine and enamel, and frequently show "Westoll lines" between

different zones of dentine deposition. One scale (PF 598, fig. 47, C) is interesting in lacking the superficial layer on the anterior part of the exposed area. This part of the scale is ornamented with bony tubercles, probably largely composed of the upper part of the cancellar layer. The more posterior part of the exposed area is covered with a layer of dentine and enamel, thin enough to show in its preserved state some suggestion of the underlying structure of the cancellar layer. Since this scale was prepared under a microscope, it is certain that the absence of the superficial layer in the anterior part of the exposed area was not due to loss in collecting or preparation; it may have been resorbed, or more probably not yet deposited in this region.

As Jarvik (1948, p. 283) has pointed out, there are "hardly any differences . . . between scales from different Osteolepid genera and species which are of sufficient importance to warrant their use in taxonomy." Thus it is not worth while to attempt to identify these fragmentary remains, and until better material is available they will be referred to as Osteolepidae indet.

As was mentioned above, fragmentary fish remains were collected in 1896 by Tower from the Late Devonian Parting Quartzite near Aspen, Pitkin County, Colorado. A few teeth in this collection were attributed to crossopterygians by Girty (Spurr, 1898, p. 21) and compared to *Rhizodus* and *Eusthenopteron*. This collection was also studied by Eastman (1904, p. 258; 1915, p. 281). In addition to the crossopterygian teeth, he mentioned some finely tuberculated plates that he attributed to arthrodires, and some smooth, perforated scales that he believed to belong to dipnoans. After seeing some of Tower's collection (although not the teeth) in the United States National Museum, and collecting near the base of the Parting Quartzite at this locality, I have come to the conclusion that all of the remains belong to an osteolepid crossopterygian. My own collections were obtained in 1949 both from the point of East Aspen Mountain, overlooking Aspen, and from the bed of Spar Gulch nearby, but the description below is based on the better preserved Spar Gulch material.

The material consists of scales and plates only. The dermal plates and most of the scales are covered with a fine tubercular ornament, with the tubercles joined more or less by ridges. Presumably these are the plates referred by Eastman to arthrodires. The scales (fig. 47, A) have a rhombic exposed area on which the tubercles are high and quite independent anteriorly, lower and

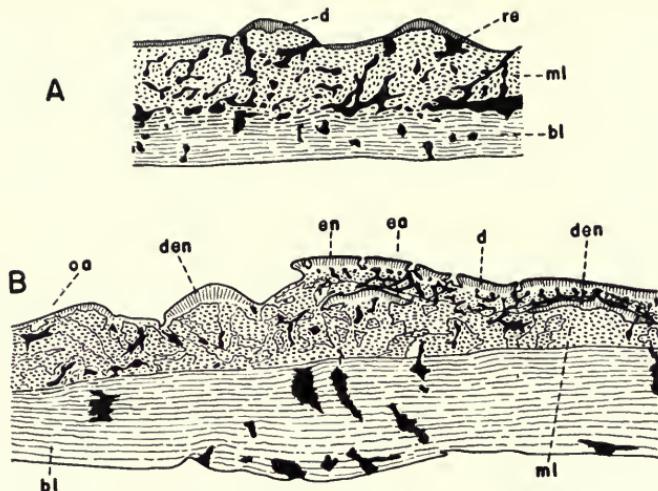


FIG. 48. Osteolepidae indet., from Aspen, Colorado ($\times 25$). A, Vertical section through dermal bone, PF 606. B, Vertical section through part of a scale, PF 604. *bl*, basal laminated layer; *d*, dentine; *den*, dentine-covered denticle; *ea*, exposed area of scale; *en*, enamel; *ml*, middle cancellar layer; *oa*, overlapped area of scale; *re*, area of resorption.

joined nearly to the top by ridges posteriorly. The overlapped area on two sides of the rhomb is relatively narrow. A thin section (fig. 48, A) reveals that there is a thick basal laminar layer and a middle cancellar layer; the tubercles are largely bone but are capped by a thin layer of dentine. A few of the scales are not tuberculate, but are covered with a smooth superficial layer in the exposed area. Presumably these are the scales that Eastman attributed to dipnoans. A thin section (fig. 48, B) of one of these scales reveals a thin, superficial layer overlying dentine-capped tubercles. The superficial layer is typically osteolepid in structure, consisting of closely spaced flat-topped denticles of dentine and enamel or vitro-dentine. It is not necessary to assume that the smooth and tuberculate types of scales belonged to different fishes. Jarvik (1948, 1950) cites a number of cases where scales are ornamented in the Osteolepidae. For example, *Gyroptychius groenlandicus* usually has a thick, shiny superficial layer on its scales, yet in one associated group of scales a few lack the superficial layer and are tuberculate (Jarvik, 1950, pl. 22, figs. 2-4); the latter resemble scales from Aspen, except that their tuberculation is finer. The scales from Aspen possessing a superficial layer of dentine overlying dentine-capped tubercles are particularly interesting (fig. 48, B). It is probable that the tubercles

were originally superficial (as they still are in most of the scales and dermal plates). The deposition of a smooth layer of dentine (and ?enamel) over earlier dentine must have involved a spreading superficially of ectodermal and mesodermal tissue. This could only have been accomplished from the regions between the tubercles where dentine had not been developed.

The reference of the remains from Aspen to the Osteolepididae is based largely on the rhombic shape of the scales, and the small overlapped area; the occasional presence of a smooth superficial layer supports this. As is the case in the osteolepids from Deadman's Creek, generic identification is not possible.

UNDETERMINED CROSOPTERYGII

A fragment of a lower jaw (PF 609) from the Darby formation on the South Fork of the Little Wind River, Wyoming, belongs to a crossopterygian but it is not more exactly determinable. The outer face is ornamented with tubercles, united at their bases, and the marginal teeth of the dentary are relatively large, striated, and probably widely spaced.

Another lower jaw of a crossopterygian (PF 602) from a limestone in the Elbert formation on Little Cascade Creek south of Columbine Lake, La Plata County, Colorado, is also undeterminable. Nearly the entire jaw is present but is poorly preserved. The external face is ornamented with tubercles, and the ramus is rather shallow. Probably this does not belong to *Holoptychius*, which is abundant elsewhere in the Elbert formation.

Bryant (Bryant and Johnson, 1936, p. 657) reported a crossopterygian from the Parting member of the Chaffee formation at Gribbles Creek, Fremont County, Colorado. Along with other crossopterygians from central Colorado, he compared it with *Glyptopomus sayrei*, but this identification cannot be accepted without confirmation.

GEOLOGICAL OCCURRENCE

Detailed geological work has been done on only small parts of the area covered in this study. However, sufficient information is available so that it is now practical to attempt a reconstruction of the conditions under which fishes were preserved in the Late Devonian of the western states. Such an attempt is useful not only as a basis for future field work but also is essential in assessing the

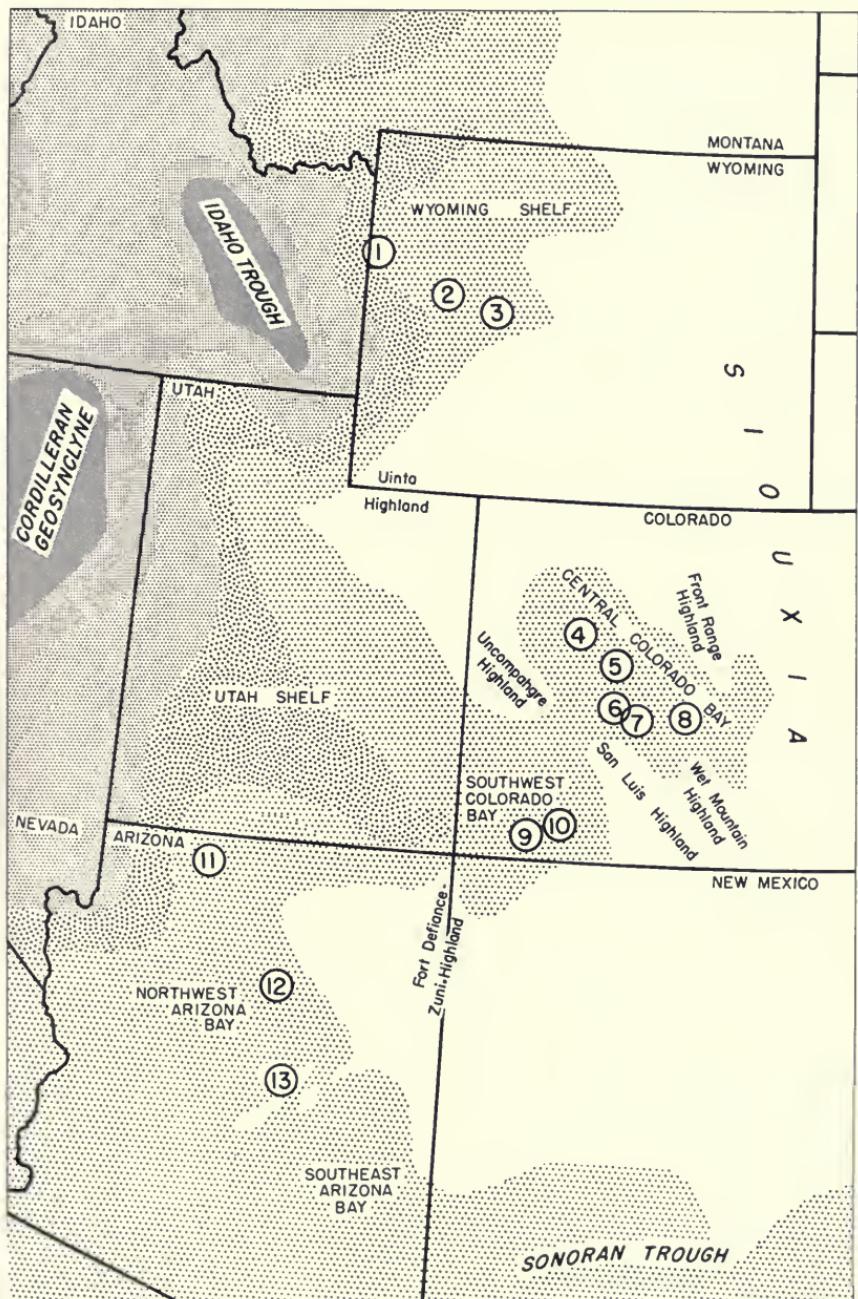
general zoological as well as the geological significance of the fish faunas.

The geological history of this region, as it may now be reconstructed from published reports is as follows: At the beginning of the Devonian (Helderberg), the seas did not cover any of this area. Presumably relief was low or moderate, since erosion without any major orogenies had been at work since the Cambrian or Ordovician. In Oriskany times, the seas advanced in the Cordilleran geosyncline, but did not overlap to any extent on to the shelf lands beyond. In Onondaga times, this sea withdrew again, and deposits of this age are found only in the Cordilleran trough in Nevada, Utah, and California.

At the beginning of the Late Devonian (Genesee) a much greater transgression began. In the Cordilleran trough of Nevada and California the *Stromatopora* zone of the Devil's Gate formation and equivalent formations were being deposited. Farther north and east, the deposition of the Jefferson formation may have started at this time in northern Utah and southeastern Idaho. The Canutillo formation of the Franklin Mountains of Texas may have heralded a similar advance of the sea in the Sonoran trough.

By Naples time, the sea had advanced farther, although it was still restricted to the geosynclines. In Nevada, the *Spirifer argentarius* zone of the Devil's Gate formation is of this age, in western Utah possibly part of the Guilmette formation, while the Jefferson formation was being deposited farther north in northern Utah, southeastern Idaho, northwestern Wyoming, and southwestern Montana. In the Sonoran trough, marine rocks of this age have been reported in northern Sonora, and the seas may have reached southern Arizona to deposit the Picacho de Calera formation.

FIG. 49. Paleogeographic map showing the maximum extent of the Late Devonian sea and the total thickness of the Devonian sediments. The encircled numbers indicate the localities at which the Late Devonian fishes discussed in this paper have been found. (1) Darby formation, Teton Pass, Wyoming; (2) Darby formation, southwestern side of Wind River Mountains, Wyoming; (3) Darby formation, South Fork of Little Wind River, near Fort Washakie, Wyoming; (4) Chaffee(?) formation, Glenwood Springs, Colorado; (5) Parting Quartzite, Aspen, Colorado; (6) Parting member, Deadman's Creek, Colorado; (7) Parting member, Fossil Ridge, Colorado; (8) Parting member, Gribbles Creek, Colorado; (9) Elbert formation, Rockwood and Little Cascade Creek, Colorado; (10) Elbert formation, Endlich Mesa, Colorado; (11) Temple Butte formation, Grand Canyon, Arizona; (12) Jerome formation, near Flagstaff, Arizona; (13) Jerome formation, near Payson, Arizona.



In the Chemung stage, the seas spread out of the geosynclines on to the bordering shelf lands and inundated land that had not been under water since Ordovician, Cambrian or pre-Cambrian times. Far from shore in the Cordilleran geosyncline, the *Philipsastraea* zone of the Devil's Gate formation and parts of the Jefferson formation and Grand View dolomite were being deposited. On the bordering shelf the sea formed shallow embayments in Wyoming, Colorado, and Arizona. On the Wyoming shelf, deposits of this age are known as the Darby formation, in the Central Colorado basin they are called the Parting member of the Chaffee formation (farther east the Williams Canyon formation may be an equivalent) and in the Southwest Colorado basin they are the Elbert formation. At the same time, the seas spread southeastward into central Arizona where the Temple Butte and Jerome formations were deposited, and also northward out of the Sonoran trough to form the Sly Gap formation in southern New Mexico and the Martin limestone in the Southeast Arizona basin. An attempt has been made in figure 49 to reconstruct the paleogeography at this time of maximum extent of the Devonian seas.

In Chautauquan times, seas remained extensive. In the Cordilleran syncline, the *Cyrtospirifer* zone of the Devil's Gate formation represents this period in Nevada, while the upper Grand View dolomite was laid down in parts of Idaho. In shallower waters, or in receding seas, the Three Forks shale succeeded the Jefferson formation in Montana, Idaho, and Wyoming. The upper part of the Darby formation of Wyoming, the Dyer dolomite member of the Chaffee formation of central Colorado, and the Ouray limestone of southwestern Colorado may be in part of this age. In the Northwestern Arizona basin, part of the Jerome formation and the Island Mesa beds are possibly Chautauquan. To the south, on the shelf bordering the Sonoran trough, the Ouray limestone is recognized in southeastern Arizona, and the Percha shale of southwestern New Mexico may be of this age (although it is considered by some to be younger).

In the latest Devonian (Conewango stage) the seas withdrew not only from the shelf but also from the geosynclines. The so-called "Three Forks with *Syringothyris*," which is attributed by some to this age, may belong to the Mississippian.

As far as I know, no fishes have been discovered in the Late Devonian rocks of the Cordilleran or Sonoran geosynclines. The limestones deposited in the open waters of the bordering shelves

contain remains of typical marine fishes such as cladoselachian sharks, hybodonts, bradyodonts, and ptyctodonts; sometimes teeth of lung fishes are discovered in such limestones. In the great embayments of the Chemung-Chautauquan sea remains of different types of fishes are common in the Darby, Chaffee (Parting member), Elbert, Temple Butte, and Jerome formations (fig. 49). The first three of these formations are very similar lithologically and are distinguished mainly by their geographical position; the Darby formation is restricted to western Wyoming and adjacent Idaho, the Chaffee formation is found only in west-central Colorado, and the Elbert formation outcrops only in southwestern Colorado. The three formations consist of a variable series of sandstones, conglomerates, shales, and limestones that are usually sandy, and often dolomitic. Cross bedding, ripple marks, mud cracks, and salt crystal casts indicate very shallow water deposition with occasional sub-aerial desiccation. Under these circumstances the large amount of clastics suggests that deposition was near to shore. Presumably the beds were deposited on beaches, mud flats, lagoons, estuaries, or river mouths on a shore of low relief; some beds may even have been deposited in fresh-water stream channels and flood plains. These formations represent a near-shore facies of the transgressing Late Devonian sea, and as such cannot be of exactly the same age wherever they occur. After the shoreline had advanced, usually more limy beds were deposited farther from shore. Thus in Wyoming the upper part of the Darby formation contains less clastic material and more limestone, with occasional crinoids. In central Colorado, the Parting member is succeeded by the Dyer dolomite of the Chaffee formation, with a marine invertebrate fauna. In southwestern Colorado, the Ouray limestone overlies the Elbert formation and has a rich marine invertebrate fauna.

Most of the fishes are found in the lower near-shore transgressive facies and are about the only fossils known from it. (The absence of invertebrates is probably due to non-preservation, for they surely existed in the near-shore environments.) As far as the geological evidence goes, all could be littoral marine fishes, but such is surely not the case. The most common genus, *Bothriolepis*, with a world-wide distribution, is everywhere characteristic of the continental "Old Red Sandstone" type of deposits. In fact, the whole order of Antiarchi is believed to have been restricted to fresh water with the exception of two highly specialized marine genera, *Grossapis* (*Ceraspis*) and *Lepadolepis* (*Ceratolepis*). *Holoptychius* is commonly

associated with *Bothriolepis* and is likewise a characteristic member of the Late Devonian, Old Red Sandstone faunas. Rhizodontidae and Osteolepididae are elsewhere found in continental deposits in the Devonian, although some of the Mississippian and Pennsylvanian genera moved into the seas. The occurrence of lung fishes, on the other hand, does not allow the assumption that they were exclusively a fresh-water group in the Devonian. *Dipterus* does occur commonly in continental deposits both in Europe and in North America, but it is found also in marine limestones, associated with marine invertebrate faunas, in some cases far from the nearest shore line. An outstanding example of a marine occurrence of *Dipterus* in this country is the Late Devonian State Quarry limestone of Iowa, which contains teeth of this genus in abundance, along with ptyctodonts and marine invertebrates. This association surely suggests that some *Dipterus* inhabited the seas, even if their teeth had been dropped in this area by a predator that had eaten them, as Eastman (1908, pp. 216-217) suggested. The two *Dipterus* teeth from the Jefferson formation, one found near Logan, Montana, and the other found on Blacksmith Fork, near Logan, Utah, occur in marine limestones, presumably deposited at some distance from the shore. In the Late Devonian, arthrodires were predominantly a marine group, although a few lingered on in rivers. Their rarity in the faunas of this region may be taken as supporting the view that the fishes came mostly from a fresh-water environment.

It would thus appear that most of the fishes of the Darby and Elbert formations, and of the Parting member of the Chaffee formation, were inhabitants of fresh-water streams and were washed after death into the edges of the advancing Chemung sea. The nature of the preservation supports the view that there was considerable post-mortem transportation of the fish remains in most cases. Generally the fossils are isolated plates, scales or fragments, obviously without any association. "Bone beds" consisting largely of worn and sorted fish fragments occur near the base of the Elbert and Darby formations; probably the beds represent concentrations by current action on the sea bottom, or by wave action on the shore. Better preservation of fishes is most unusual in these Late Devonian sediments. At certain horizons in the Parting member on Deadman's Creek, Gunnison County, Colorado, there are abundant remains of *Litoptychus bryanti*, including many entire bones as well as jaws and large parts of skulls. It is possible that these remains represent elements of one or a few individuals, although association has not been demonstrated. If, as seems probable,

there was less transportation in this case, the thin-bedded sandy limestones in which the fish occur were probably deposited near shore, perhaps near a river's mouth. The only articulated remains that have been found are intact, though poorly preserved, shields of *Bothriolepis coloradensis*. They were collected by Cross near Rockwood, and I also collected them ten feet above the base of the Elbert formation, two miles southeast of Devon Point, Endlich Mesa. Both localities are in La Plata County, Colorado. The sandstone in which they occur may not be marine, but a deposit in the stream in which the *Bothriolepis* lived.

From one locality in the Central Colorado basin has been reported a fish fauna containing definite marine elements. It occurs twenty feet above the base of the Parting member of the Chaffee formation, on Gribbles Creek, Fremont County, Colorado (Bryant and Johnson, 1936). Remains of an undetermined crossopterygian and a tooth of *Dipterus* may be of fresh-water origin, but the arthrodire plate fragments more probably belonged to marine fishes, and this is surely the case with the cladoselachian shark, *Ctenacanthus*, and the bradyodont, *Sandalodus*. These fragments are the only clear record of marine fishes in the Colorado and Wyoming embayments.

Little information is available on the Devonian geography of the Grand Canyon region of Arizona. The Temple Butte formation was deposited on a rugged surface with as much as 100 feet of relief. Fishes have been found for the most part in its basal sandstones and conglomerates. Considerable limestone occurs, although it is often sandy, and in it a few casts of marine invertebrates have been discovered. It seems probable that this is a near-shore facies, deposited in the advancing Chemung sea. Then the only fishes reported, *Bothriolepis* and *Holoptichius*, must have been transported from a nearby land. Since the Paleozoic rocks of northern Arizona and southern Utah are nearly completely buried below later rocks of the Colorado Plateau, little can be said about the position and configuration of this land that must have existed nearby. According to McKee (1951, pl. 1, fig. B) a large promontory projected from the Defiance-Zuni positive area, northwestward between the Southwest Colorado basin and the Northwest Arizona basin (fig. 49).

The fauna of the Jerome formation of central Arizona is related stratigraphically and faunally to those faunas described in this paper. Deposition in this region occurred near a steeper, rockier shore, and probably for this reason there is a larger admixture of marine fishes. This fauna will be discussed in a later paper.

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